Mt. Graham red squirrel use of forest habitat:
Historical, present, and future perspectives

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Abstract

Geographically isolated populations of endangered species such as the Mount Graham red squirrel (MGRS) (*Tamiasciurus hudsonicus grahamensis*) are particularly sensitive to fluctuations in habitat quality and extent. In recent decades a series of insect outbreaks and high-severity fires degraded the sole MGRS habitat in the Pinaleño Mountains of southeast Arizona, and have raised concerns about the long-term viability of the species. In this study we use dendrochological and spatial analysis methods to reconstruct the history of MGRS habitat size and quality over the past three centuries to provide historical context for current habitat conditions. We found that EuroAmerican land uses starting in the late 1800s excluded fire from the mixed-conifer forest, resulting in a significant expansion of suitable MGRS habitat over the next century. Suitable habitat at the start of the MGRS monitoring program in 1989 was greater than at any time in the reconstructed period. Prior to EuroAmerican settlement, habitat would have been limited primarily to the spruce-fir forest by the frequency and severity of fires burning in the mixed-conifer forest at the ecotone between spruce-fir and mixed-conifer forest types. The spruce-fir and mixed-conifer forests burned in a large, high-severity fire in 1685, resulting in a much greater reduction in suitable habitat for MGRS, lasting several decades, than has been experienced by the contemporary squirrel population. Recovery of the MGRS population following the 1685 fire suggests that MGRS is highly resilient to significant habitat degradation. Recent disturbances had the greatest effects on spruce-fir forest and forecasts of future temperature and precipitation conditions suggest a decline in suitable conditions for this forest type. Over the past century MGRS populations have adapted to mixed-conifer forest, which now hosts the majority of active middens and nests. If historically-associated habitat in the spruce-fir forest continues to decline, the mixed-conifer forest may provide suitable resources for MGRS if exclusion of fire from these sites continues.

Contents

Introduction

   The Mount Graham red squirrel (MGRS) (*Tamiasciurus hudsonicus grahamensis*) is a federally listed subspecies endemic to a single mountain range in southeastern Arizona. Within its home range in the Pinaleño Mountains, MGRS midden (Smith and Mannan 1994, Merrick et al. 2007) and nest locations are strongly correlated with dense stands of mature, large diameter conifers with a high proportion of corkbark fir (*Abies lasiocarpa* var. *arizonica* (Hook.) Nutt.). High stand densities limit exposure of squirrels to aerial predators (Schauffert et al. 2002, Rushton et al. 2006) and mature stands with abundant corkbark fir are indicators of sites with infrequent fire that provide abundant seeds (Burns and Honkala 1990) and cool moist conditions and accumulated coarse woody debris provide appropriate conditions for edible fungi (Harmon et al. 1986) and cone storage (Zugmeyer and Koprowski 2009). Potential MGRS habitat meeting these conditions exceeded 12,000 ha prior to the 2004 Nuttall-Gibson fire (Hatten 2000), although, the area used actively by the ~ 300 squirrels was significantly smaller (Koprowski et al. 2005). Active use of middens by MGRS in mixed-conifer was equivalent to use in spruce-fir forest prior to 1996. However, after a decade of insect outbreaks and two mixed-severity fires, MGRS activity decreased markedly in the spruce fir (Koprowski et al. 2005, Zugmeyer and Koprowski 2009). These disturbances reduced seed production and created abundant canopy gaps that facilitated predation by Mexican spotted owl (*Strix occidentalis lucida*) and other avian predators.

   Damage to the spruce-fir forest initiated with an outbreak of an endemic looper moth (*Nepytia janetae* Rindge) that caused defoliation to all life stages of spruce and corkbark fir from 1996 - 1999 (USDA Forest Service 2000). Weakened host defenses

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likely contributed to subsequent outbreaks of spruce beetle (*Dendrochtonus rufipennis* Kirby) and western balsam bark beetle (*Dryocoetes confusus* Swaine) from beetle populations that established following a winter ice storm in 1993. Damage to spruce needles continued with the introduction of spruce aphid (*Elatobium abietnum* Walker), in 1999 (Lynch 2009). Although *N. janetae* and spruce aphid can be lethal, the majority of host tree mortality can be attributed to spruce beetle and western balsam bark beetle activity (Lynch 2004).

During the *N. janetae* outbreak from 1996-1999 high numbers of looper larvae may have served as an additional source of nutrition that increased survivorship of MGRS (Lynch et al. 2009), resulting in a short-term population increase prior to declines caused by loss of surviving spruce and corkbark fir. Direct mortality of MGRS in the 2004 Nuttall-Gibson fire was low (Leonard and Koprowski 2010); however, the loss of canopy cover and increased exposure to predators as a result of foraging in insect and fire-created gaps caused a steep decline in MGRS survivorship relative to less impacted areas after 2002 (Zugmeyer and Koprowski 2009).

The combination of insect outbreaks and fire reduced the extent of spruce-fir forest by 66% and significantly reduced the area and quality of suitable MGRS habitat (Koprowski et al. 2005, Zugmeyer and Koprowski 2009). Total MGRS census counts in December 2012 were approximately 18% of the total count recorded in December 1995 prior to the series of disturbances to MGRS habitat (CRL 2014).

Prior to the onset of fire exclusion in the mid-1870s (Bahre 1998), MGRS habitat was likely restricted to the spruce-fir forest and small fire refuge sites. Prior to the 2004 fire, the only known high-severity fire affecting the spruce-fir forest occurred in 1685

(Grissino-Mayer et al. 1995, Swetnam et al. 2009, Margolis et al. 2011). The 1685 fire was stand-replacing over most of the spruce-fir and much of the surrounding mesic mixed-conifer forest but was low to moderate-severity in fuel-limited dry mixed-conifer and pine dominated forest (O'Connor 2013). Prior to 1870, median fire return intervals in mesic mixed-conifer forest surrounding the spruce-fir zone ranged from 17-44 years and had a strong influence on forest structure and species composition (O'Connor 2013). Fire in mixed-conifer forest sustained open canopy conditions, low stem densities, and infrequent occurrence of heat-sensitive spruce and corkbark fir.

In this study we reconstruct spatial and temporal dynamics of forest conditions associated with MGRS habitat over three centuries of fire, spruce beetle outbreaks, and human land uses. Changes over time to the size and spatial distribution of MGRS habitat may provide insight into resilience of MGRS populations to habitat loss following major disturbance events such as the 1996-2004 insect outbreak and fire events. Placing the current extent of suitable MGRS habitat into a historical context is useful as a measure of current threats to species survival and for determining management options best suited to long-term stability of future habitat.

Study area

The spruce-fir and mixed-conifer forests of the Pinaleño Mountains are situated at the top of ecological and elevational gradients of more than 2,100 meters from 3,267 m in spruce-fir forest down to desert grasslands at 1,150 m (McLaughlin 1993). The study area is populated primarily by Engelmann spruce (*Picea engelmannii* Parry ex. Engelm.) and corkbark fir (*Abies lasiocarpa* var. *arizonica* (Hook.) Nutt.) above 2,985 m

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(9,800 ft), transitioning at lower elevation to mesic mixed-conifer forest with additional components of Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Mirbel) Franco), southwestern white pine (*Pinus strobiformus* Engelmann), and aspen (*Populus tremuloides*). The forest surrounding the study area along the central plateau of the range is primarily dry mixed-conifer forest that also includes white fir (*Abies concolor* (Gor. & Glend.) Lindl. ex Hildebr.) and ponderosa pine (*Pinus ponderosa* var. *scopulorum* Engelmann). On steep slopes below 2,135 m (7,000 ft), mixed-conifer forest transitions abruptly to Madrean pine-oak forest (*Quercus* spp.) (McLaughlin 1993). Relatively pure stands of ponderosa pine occur infrequently.

A fire burned through most of the spruce-fir forest and parts of the surrounding mesic mixed-conifer forests with high severity in 1685 (O'Connor 2013). Small patches of surviving spruce and fir began repopulating the upper elevation forest shortly after the fire, and much of the spruce-fir zone was under closed canopy conditions by the mid to late 1700s (O'Connor 2013). No fires entered into the spruce-fir forest for 311 years until the Clark Peak fire in 1996 burned a small area (91 ha: 10%) of the upper elevation spruce-fir forest with high severity. Shortly thereafter the 2004 Nuttall Complex fire burned through 472 ha (52%) of the remaining spruce-fir forest with more than 98% moderate to high canopy burn severity.

Methods

We reconstructed spatiotemporal dynamics of suitable MGRS habitat by dendrochronological reconstruction of tree population demographics and fire events (O'Connor 2013), and evaluation of the reconstructed forest conditions at various times

for suitability with respect to forest conditions known to support MGRS (Smith and Mannan 1994, Merrick et al. 2007).

Forest species demography

To reconstruct forest condition through time, we sampled forest demography material using a grid of 58 fixed-area 0.05-ha plots spaced 1 km apart over the area above 2,135 m (7,000 ft). Trees greater than 19.5 cm diameter at breast height (DBH) were sampled over the full plot area, trees <19.4 cm were sampled in a sub-plot equal to one third the total plot area (0.017 ha). In the area above 2,835 m (9,300 ft), containing 75% of known MGRS midden locations, we installed a second fixed-sample size grid with an additional 21 locations offset 500m from the original sampling grid. The second grid was used to increase spatial resolution of reconstructed forest disturbances and changes within the core MGRS habitat. In fixed-sample size plots, the 10 spruce and 10 non-spruce >15 cm DBH nearest to plot center were sampled. In all plots, up to three increment cores were removed from live trees within 20 cm of mineral soil. Trees less than 1 cm DBH were cut at the soil surface. Radial cross-sections were collected from stumps and fallen logs, and quarter round wedges were removed from snags as close to the root collar as possible.

Increment cores were dried and stored in paper straws prior to mounting and surfacing. Cut sections were trimmed and mounted to plywood backing if necessary, and then sanded with progressively finer grits until individual cell structure was observable (usually 400 grit). Samples were cross-dated using a combination of visual pattern matching (Yamaguchi 1991), and skeleton plots (Stokes and Smiley 1968). The

master chronology developed from Douglas-fir within the spruce-fir zone had the highest series inter-correlation among all high elevation species and was used to validate crossdating. On samples that did not include pith, concentric ring pith locators (Applequist 1958) were used to estimate pith dates if ring curvature indicated pith was within 10 years of the innermost ring. Ring-width measurements were recorded with J2X measuring software on a Velmex TA system® with sensor accuracy of one micron (VoorTech 2010). Crossdating of individual trees was checked with COFECHA crossdating analysis software (Holmes 1983). Cores that did not correlate with the plot-level chronology at a level of 0.3 or higher were removed from the analysis (Grissino-Mayer 2001).

Demographic reconstruction of seedling recruitment was based solely on fixed-area demography plot data. Recruitment dates from trees with DBH 19.4 cm or smaller were used in triplicate to account for their collection on only 1/3 of the total plot area. Recruitment dates were binned by 5-year intervals to account for variability in sampling heights.

Fire history

To reconstruct fire history we collected fire-scarred material from live trees, snags, and stumps within the demography plots and while traveling among plots. All fire-scarred samples collected outside of demography plots were georeferenced and site characteristics were recorded and photographed. When appropriate, several samples from individual stumps and snags were collected to preserve as many fire

dates as possible (Dieterich and Swetnam 1984). Material was processed in the laboratory as described previously.

On fire-scarred samples we recorded inner ring or pith date, year and season of fire, outer year or bark date, and any undetermined scar or growth suppression dates. Scars of undetermined origin, injury-related growth suppressions, and outer ring dates corresponding to fire scars recorded within 500 m of a sample were recorded as fire dates; otherwise they were excluded from fire history analyses.

Spatial reconstruction of 1685 post-fire forest recolonization

The 1685 stand-replacing fire catastrophically reduced suitable MGRS habitat. We reconstructed the size of the immediate post-1685 spruce- and corkbark fir-inhabited area and subsequent spatial progression of tree establishment in the burned area to determine the post-disturbance expansion of potential MGRS habitat. An interpolated surface of spruce and corkbark fir establishment progression was generated through inverse distance weighting of earliest establishment dates from the four nearest plots with a power function of two (ESRI Inc. 2012). Establishment dates were based on the minimum inner ring date if pith was not present or estimable within 10 years.

Midden density surface

We estimated the historical potential of the forest to support MGRS by evaluating contemporary forest conditions associated with MGRS midden frequency, and then quantifying the areas matching those conditions at different points in the past. We used

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a density of >0.5 middens per hectare to identify sites likely to have been occupied by MGRS for multiple generations; this value is based on a mean summer core range of 2 hectares per individual and territoriality behavior that reduces overlap of active squirrel core ranges (Koprowski et al. 2008). Sites with midden density exceeding 0.5 middens per hectare contain both active and legacy middens, and were used as a proxy for long-term occupancy of the site by MGRS. We used midden locations from the 1996 squirrel midden survey to generate a midden density surface for conditions just prior to recent insect and fire disturbances. The midden density surface was constrained to include only sites located within 250 m of known middens to reduce potential of over-estimating midden density area. Calculated midden densities were classified as low density (below 0.5 middens/ha), moderate density (0.5-1 midden/ha), and high density (>1 midden/ha). The midden density surface was then overlaid on the map of historical fire frequency to examine spatial relationships between long-term site occupancy and historical fire frequency.

Spatial reconstruction of fire frequency

To create a fire frequency surface covering the upper elevation forest types in and around MGRS midden locations, we used the 1-km demography sampling grid to composite all fire records collected within 500 m of a demography plot location (Dieterich 1980, Farris et al. 2010). Composite records were filtered to include only fires recorded on two or more trees. A composite record of fire years from multiple samples over a discrete spatial unit produces a more complete record of fire occurrence because individual trees and samples are imperfect recorders of fire, and scars are often eroded or burned off in subsequent events (Dieterich 1980, Dieterich and Swetnam 1984).

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Compositing of fire records assumes topographic and ecological homogeneity within the specified scaling unit. While homogeneity at the kilometer scale cannot be assumed for all forest types and across the vertical gradient sampled in the Pinaleño Mountains, variability among one km^2 gridded cells was assumed to be greater than variability within cells.

Fire frequency was calculated for each composited plot by dividing the sum of fire events by the number of years in the analysis period. A fire frequency surface was then interpolated over the sampled area to identify patterns of fire frequency in relation to forest types, landscape features, and period of analysis. Interpolation was based on inverse distance weighting of four nearest point locations with a power function of two and a raster cell size of 30 m (ESRI Inc. 2012). We used the pre-EuroAmerican settlement fire frequency surface (1640-1880) to determine MGRS midden location preference as a function of mean fire return interval (MFI).

Results

A dominant pattern in the forest demography and fire datasets is the major increase in successful seedling recruitment and associated increased stem densities in the mixed-conifer forest following the fire exclusion in the mid-1880s. Seedling recruitment per five-year interval rarely surpassed 10 stems per hectare prior to 1900. After 1900, five-year seedling recruitment increased 600-1000%, averaging more than 50 stems per hectare from 1920 to 1955. Exclusion of fire followed by increased abundance of shade-tolerant species resulted in improved foraging conditions and food resources for MGRS throughout much of the high elevation mesic mixed-conifer forest

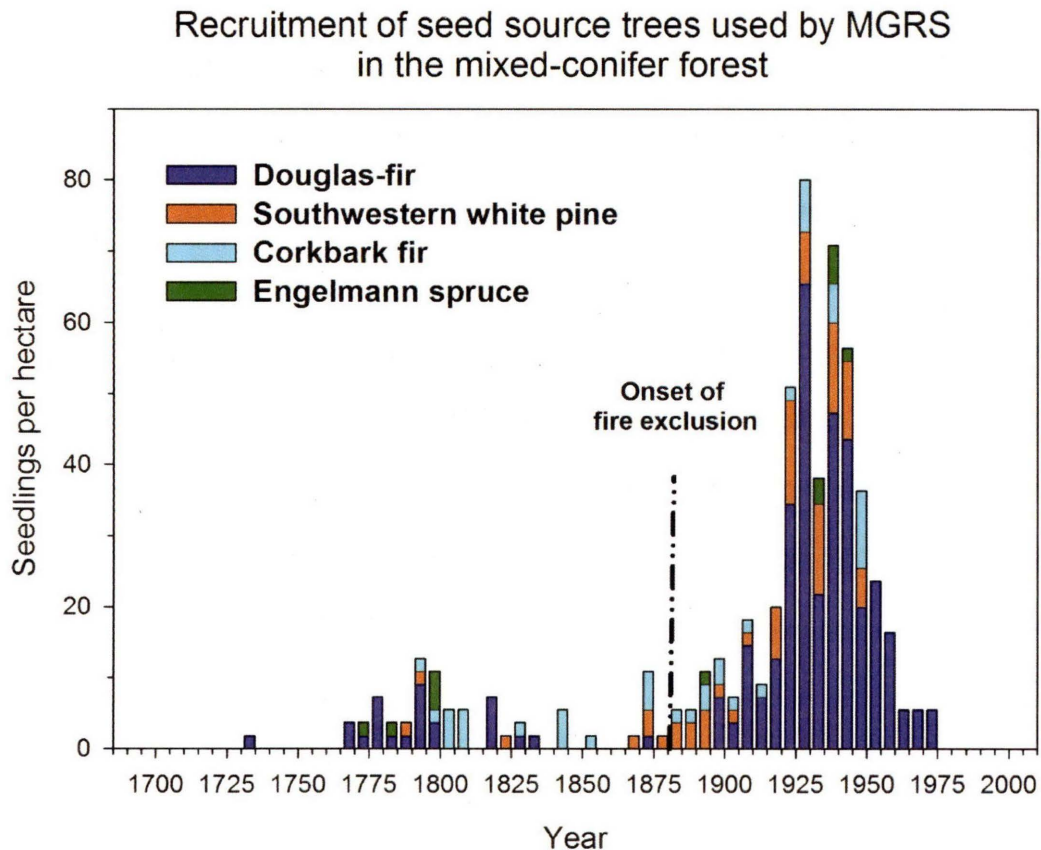(Figure 1From 1870 to 1996 mean stem densities increased more than 2,300% (range of 65%-10,500%).

Figure 1 Seedling recruitment in mixed-conifer forest 1685 – 2008.
Increase in seedling recruitment after 1880 coincides with EuroAmerican settlement and the interruption of pre-settlement fire regimes (N= 11, 0.05 ha plots). Increased stem densities following fire exclusion may provide improved MGRS habitat quality in the mesic mixed-conifer forest. Low seedling recruitment after 1970 suggests that the mixed-conifer forest was fully stocked after this time.

In contrast to the abrupt increase in seedling recruitment and stand densities observed in the mixed-conifer forest following fire exclusion, seedling recruitment and species in the higher elevation spruce-fir forest were not affected by fire exclusion. No

fires occurred in the spruce-fir forest between 1685 and 1996, so the effects of anthropogenically-driven fire exclusion were restricted to vegetation communities located below the spruce-fir along the elevational gradient. Seedling recruitment in the spruce-fir zone in the first 150 years following the 1685 stand replacing fire was dominated by Engelmann spruce and corkbark fir with minor components of Douglas-fir and southwestern white pine. Over the whole of the reconstructed period, seedling recruitment averaged 15 stems per five-year interval, with a range of 0-50. After 1860, shade-tolerant spruce and corkbark fir were the primary species recruiting, though occasionally aspen continued to recruit in individual sites until 1920. Similar to the record from mixed-conifer plots, no recruitment of any species was recorded in spruce-fir plots from 1975 to 2004, suggesting that resources for understory recruitment were saturated in high-elevation sites prior to the 2004 fire.
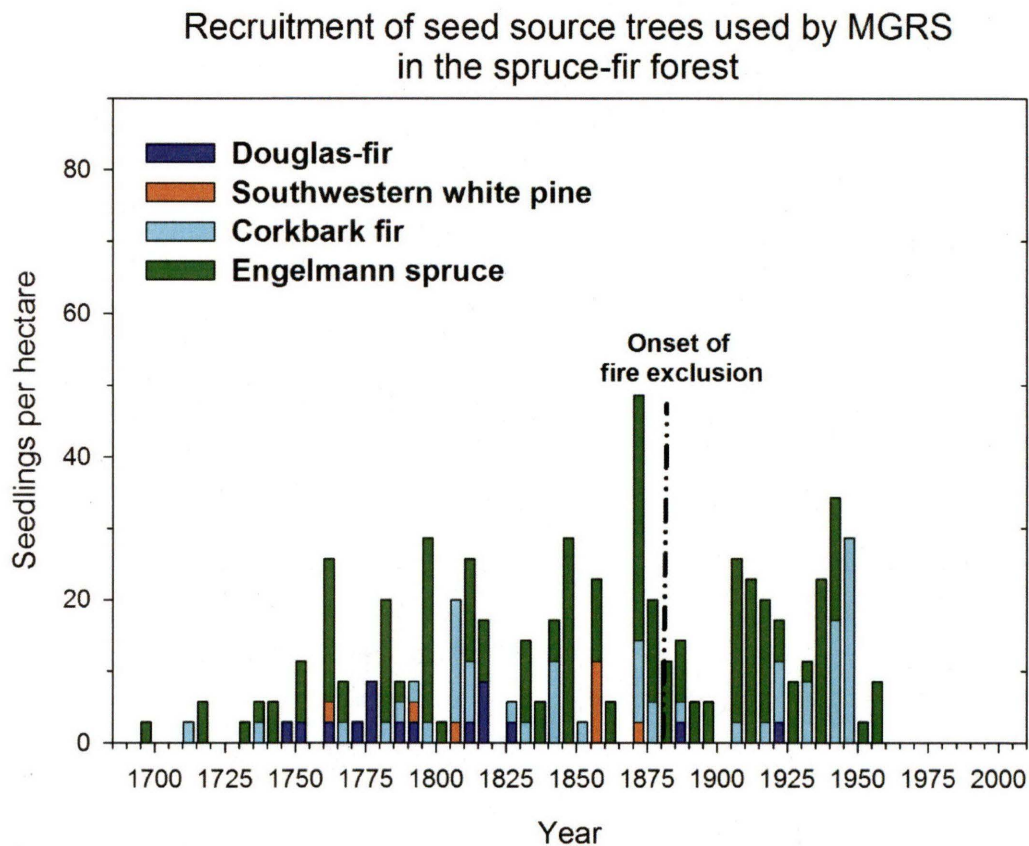
Recruitment of seed source trees used by MGRS in the spruce-fir forest

Figure legend:
- Douglas-fir
- Southwestern white pine
- Corkbark fir
- Engelmann spruce

Onset of fire exclusion

Y-axis: Seedlings per hectare

X-axis: Year

Figure 2 Seedling recruitment in spruce-fir forest from 1685 through 2008. Seedling recruitment demonstrates periodic pulses related to disturbance from spruce beetle outbreaks (N = 6, 0.05-ha plots). In contrast to the mixed-conifer forest, recruitment does not appear to be affected by EuroAmerican settlement in the 1880s. A trend of increasing domination of recruitment by corkbark fir and Engelmann spruce can be seen by the mid-1800s. Low seedling recruitment after 1950 suggests that the spruce-fir forest was fully stocked prior to the series of insect outbreaks and fires of the 1990s.

Spruce and corkbark fir recovery following 1685

For the first fifty years following the high-severity fire in 1685, spruce seedling

establishment was limited to four small refuge populations totaling fewer than 200 ha

(Figure 3, Table 1). By 1870, the area occupied by Engelmann spruce exceeded 900

ha, representing the maximum extent of the spruce-containing forest prior to the onset

of fire exclusion at lower elevations. Over the next 33 years, Engelmann spruce and corkbark fir aggressively colonized mixed-conifer areas where fires were excluded, nearly doubling their occupied area (Figure 3 & 4). Spruce and corkbark fir extent continued to increase throughout the 20th century fire-free interval, eventually reaching a maximum extent of more than 2, 200 ha by the mid-1970s.
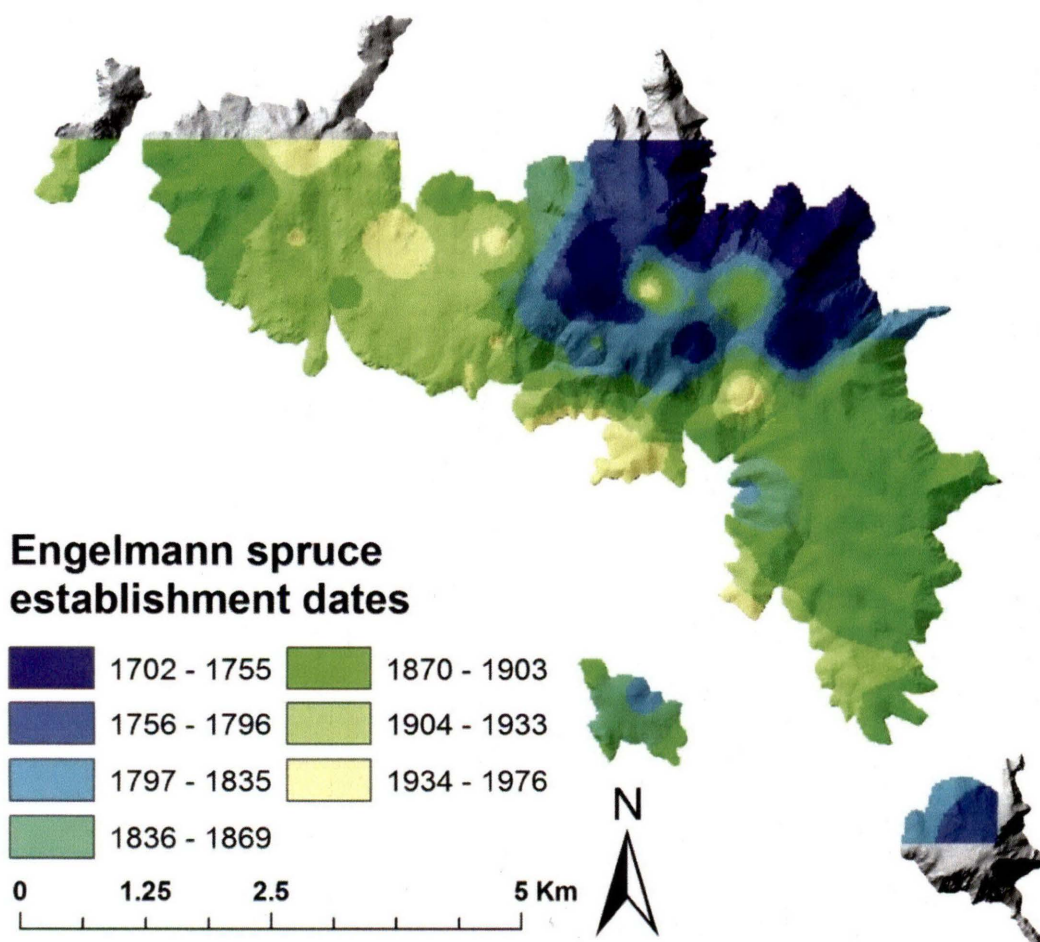

Engelmann spruce establishment dates

1702 - 1755	1870 - 1903
1756 - 1796	1904 - 1933
1797 - 1835	1934 - 1976
1836 - 1869	

0   1.25   2.5   5 Km

N

Figure 3 Temporal progression of Engelmann spruce establishment following the stand replacing fire in 1685. The map extent is limited to the forested area above 2,835 m elevation. The age surface is interpolated from 44 gridded point locations. The interpolation is based on an inverse distance weighting algorithm that uses four nearest point locations with a power function of two (O'Connor 2013).

The maximum spatial extent of corkbark fir (705 ha) and Engelmann spruce (913 ha) in 1870 probably reflects the approximate size of the cool, moist forest type unaffected by fires in surrounding forest types in the 200 years between the 1685 stand replacing fire and exclusion of fire in the mixed-conifer in the mid-1880s.
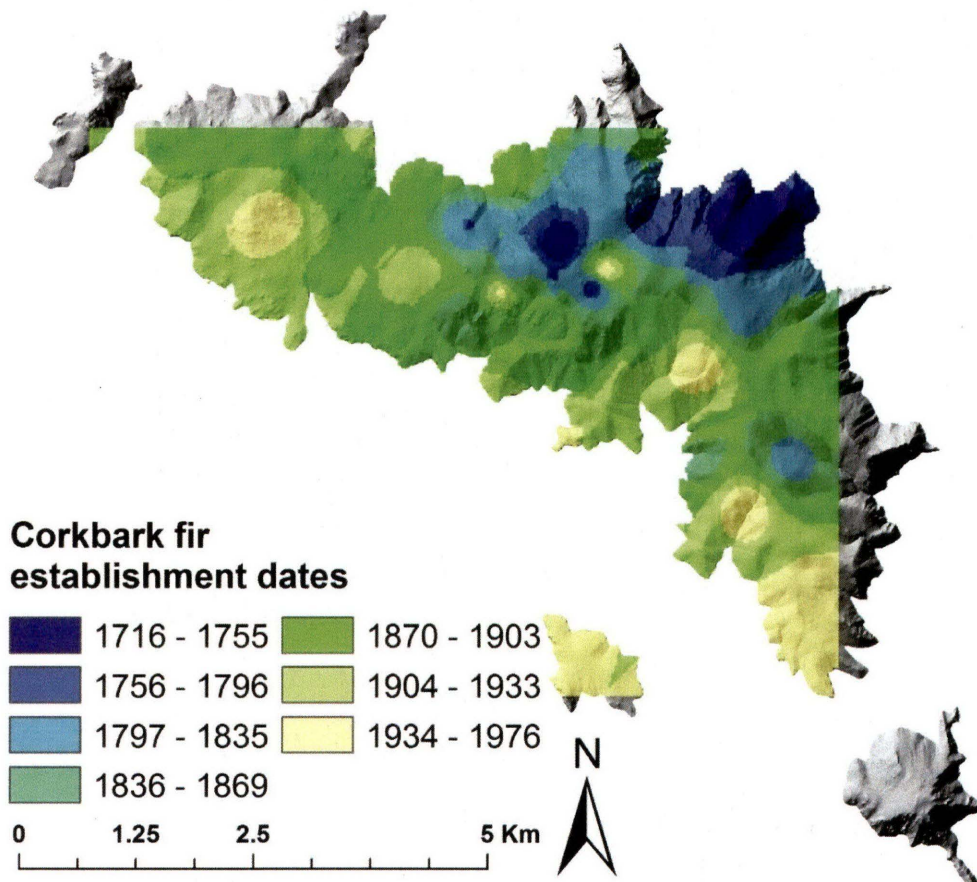

Corkbark fir establishment dates

1716 - 1755	1870 - 1903
1756 - 1796	1904 - 1933
1797 - 1835	1934 - 1976
1836 - 1869	

0   1.25   2.5   5 Km

N

Figure 4. Temporal progression of corkbark fir establishment following the stand replacing fire in 1685. The map extent is limited to the forested area above 2,835 m elevation. The age surface is interpolated from 37 gridded point locations. Spatial interpolation is based on an inverse distance weighting algorithm that uses four nearest point locations with a power function of two (O'Connor 2013).

Table 1. New and cumulative area occupied by corkbark fir and Engelmann spruce after a high-severity fire in 1685, at 40-year intervals and in 2008. The area occupied by corkbark fir (ABLA) and spruce (PIEN) is a proxy for MGRS habitat in the area where fire was naturally excluded.

Year	ABLA		PIEN	
	New ha	Cumulative ha	New ha	Cumulative ha
1755	71	71	190	190
1796	123	194	233	423
1835	242	436	238	661
1870	269	705	252	913
1903	686	1,391	731	1,643
1933	457	1,848	498	2,141
1976	249	2,096	196	2,337
2008	-1,308	**788**	-1,308	**1,029**

Midden density surface in relation to fire and forest recolonization

Locations of 1,033 middens recorded in the 1996 midden census (CRL 2014) were used to develop a midden density surface for the 2,718 ha used by MGRS at that time. The squirrel population from 1989 to 2013 peaked from 1995 to 1996 (CRL 2014). The area where midden density exceeded 0.5 middens per hectare (949 ha) is approximately one third of the total area occupied by MGRS in 1996 (Figure 5, Table 1).
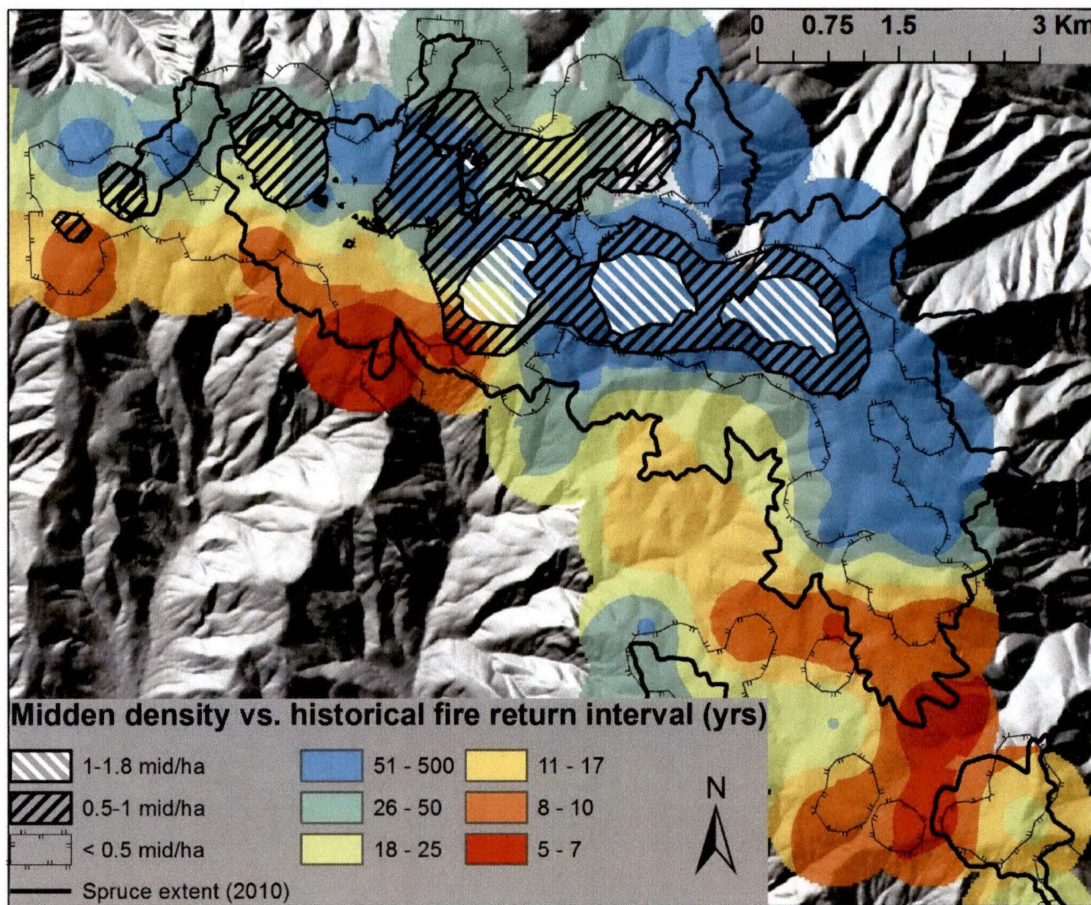
Figure 5. Midden density during 1996 with respect to historical (pre- fire exclusion) fire frequency. The fire frequency surface is based on inverse distance weighting of 53 composited 1-km^2 sites using four nearest neighbors and a power factor of two. Fire frequency is calculated from 104 spatially reconstructed fire events recorded in two or more sites from 1640-1880 (O'Connor 2013).

Areas where midden density exceeded 0.5/ha tended to be located where historical mean fire return interval (MFI) was greater than 33 years (89% of sites), and usually (64% of sites) where MFI exceeded 100 years (Table 2). In the 204 ha area where midden density exceeded 1 midden/ha, 77% of sites had historical fire return intervals greater than 100 years, and 92% had historical fire return intervals greater than 33 years.

Table 2. Mount Graham red squirrel midden density in relation to historical mean fire return interval (MFI). Percentage values are the proportion of low, moderate, and high midden density sites located in areas with prolonged fire-free periods prior to EuroAmerican settlement (1640-1880) (Figure 5).

MFI (years)		< 33	> 33	> 100
Midden Density	middens/Ha	% of sites	% of sites	% of sites
Low	< 0.5	53	47	28
Moderate	0.5 - 1	12	88	60
High	> 1	8	92	77
Mod+High	> 0.5	11	89	64

The 1996 midden survey identified low-densities of MGRS middens throughout the mixed-conifer forest (supplemental figures S-1 and S-2), although high midden densities were consistently associated with the long-term presence of spruce and corkbark fir (Table 3A). During the EuroAmerican settlement period, when extent of spruce and corkbark fir doubled in approximately 30 years (from 1870-1903), sites with high midden density were most strongly associated with the spatial distribution of corkbark fir (Table 3B). Prior to EuroAmerican settlement and fire interruption, sites with high midden density were more strongly associated with the distribution of Engelmann spruce (Table 3C).

Table 3 Mount Graham red squirrel midden density in relation to historical extent of Engelmann spruce and corkbark fir. Percentage values in 1976 (yellow) are the proportion of total midden area occurring within forest containing spruce (PIEN) and corkbark fir (ABLA). Percentage values in 1903 (green) and 1870 (blue) represent the proportion of midden density classes found in sites occupied by corkbark fir and spruce in early fire exclusion and pre-fire exclusion periods respectively.

| | | Proportion of midden area (%) | | | | | |
| | | A. 1976 | | B. Pre 1903 | | C. Pre 1870 | |
Midden Density	Middens/ha	ABLA	PIEN	ABLA	PIEN	ABLA	PIEN
Low	< 0.5	42	47	56	72	24	29
Moderate	0.5 - 1	66	66	91	62	37	47
High	> 1	95	93	83	69	64	64
Mod+High	> 0.5	72	72	89	64	44	52

The majority of the area with midden density exceeding 0.5 middens/ha, an estimate of pre-fire exclusion MGRS habitat, experienced moderate to high fire severity in 1685 (Figure 6A). Small patches of mature spruce, corkbark fir, Douglas-fir, and southwestern white pine, important seed sources for MGRS (Froehlich 1990), are known to have survived within the high-severity extent of the 1685 fire (O'Connor 2013). The post-1685 MGRS population would likely have been dependent upon these small patches for several decades following the fire.

Recent fires negatively affected MGRS habitat, but to a lesser degree than the 1685 fire because active fire suppression efforts prevented the entire spruce-fir community from burning. The recent fires had a greater proportion of mixed- and high-severity burn patches than the 1685 fire (O'Connor 2013) but more than 1,000 ha of spruce and fir-containing forest were not burned (Figure 6B). Several areas of highest midden density remain unburned by recent fires, although many of these sites are located within the core spruce-fir zone that experienced significant insect-caused mortality, which degraded MGRS habitat quality (Koprowski et al. 2005).
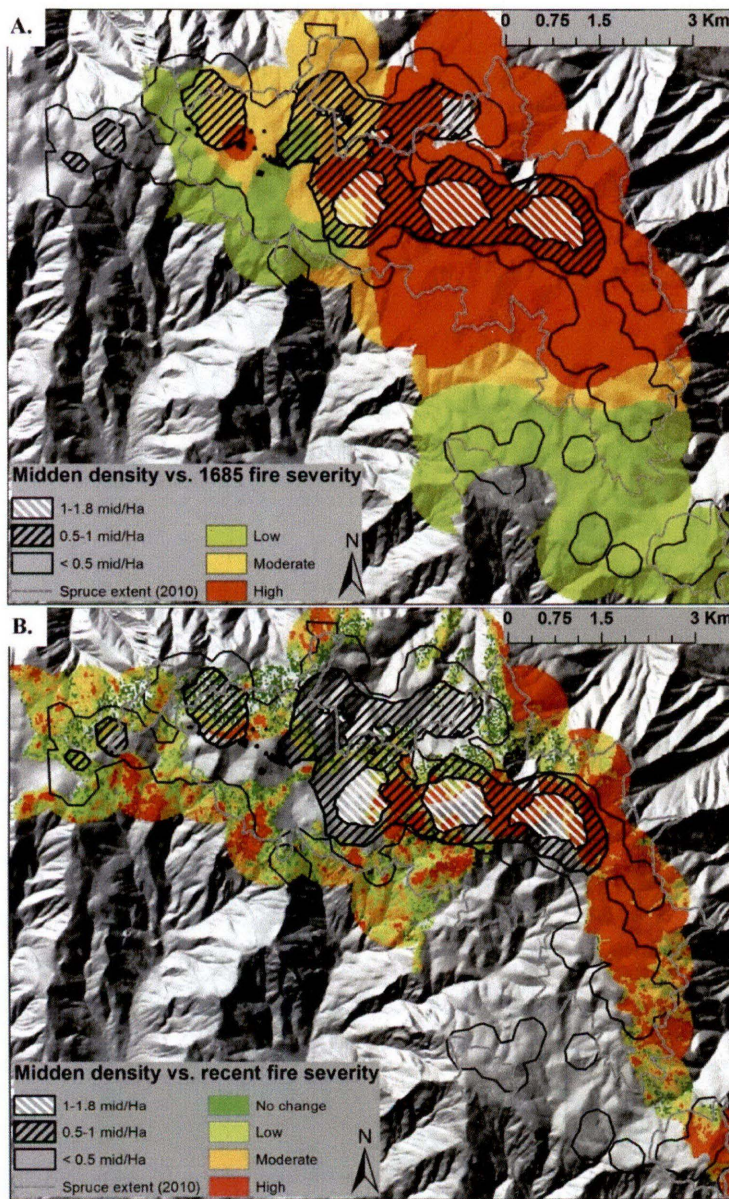
Figure 6. Mount Graham red squirrel core habitat in relation the 1685 fire and recent stand-replacing fires. The 1685 fire severity is reconstructed from fire scars and post-fire seedling recruitment from 53 point locations (Part A.). The fire severity surface is interpolated with inverse distance weighting of four nearest neighbors with a power function of two. Recent fire severity classes are generated from reclassified relative difference normalized burn ratio (rdNBR) from the MTBS database (MTBS 2013) using the method of Miller and Thode (2007) (Part B.). Fire spatial extents are clipped to the study area.

Discussion

The size and quality of habitat suitable for use by MGRS has changed

significantly over the past several centuries. At the start of squirrel monitoring efforts in

1989, more high-quality habitat was available than at any time in the 300-year historical

reconstruction. Suitable habitat peaked in 1995 as the result of more than a century of

fire exclusion from mixed-conifer forests surrounding the spruce-fir zone. High midden

density within the spruce-fir forest zone suggests that multiple generations of MGRS

used these sites prior to expanding into mixed-conifer forest in response to fire

exclusion. Exclusion of fire from mixed-conifer forests led to an infilling of forest

understory with shade tolerant species and eventual canopy closure that would have

limited predation by aerial predators and increased stand density. In addition, the

elimination of spreading fires increased the residence time of fallen logs and other

substrates for fungal reproduction, further enhancing food resources for MGRS (Young

et al. 1997). The century of structural and species changes in mixed-conifer forest

facilitated dispersal of MGRS midden sites throughout the mixed-conifer forest where

some midden locations occurred along the edge of the mixed-conifer-Madrean pine-oak

ecotone on sites that experienced frequent fire prior to EuroAmerican settlement. Even

with the significant expansion of available habitat, high midden densities suggest that

the spruce-fir forest remained the preferred habitat for MGRS into the mid-1990s.

The series of insect outbreaks and fires in the spruce-fir zone that began in 1996

significantly altered habitat quality of MGRS by reducing food resources and shelter

from predators (Koprowski et al. 2005, Koprowski et al. 2006). Current MGRS habitat

quality and extent within the spruce-fir zone has been reduced to approximately 1,030

ha, a decline of 56% from 1996 levels. Mixed-conifer forest surrounding the spruce-fir zone was largely unaffected by the 1990s insect outbreaks and large areas were untouched by the 1996 and 2004 fires, though spruce aphid and mountain pine beetle have had some effects in this forest (Lynch 2009, Lynch and O'Connor 2013). Much of the current mixed-conifer forest has not experienced fire for more than a century (O'Connor 2013), suggesting that optimum habitat for MGRS may have shifted to mixed-conifer forest for at least the next several decades depending upon the ability of the spruce-fir forest to recover under warmer and drier conditions than the post-1685 period.

Suitable habitat for MGRS has been through significant reductions in the past, most notably following the high-severity fire in 1685. Fewer than 200 ha of suitable spruce-fir and mesic mixed-conifer forest appear to have survived the 1685 fire. The fire would have extremely reduced available food resources, structural components that provide nest and midden locations, and escape cover from predators, probably resulting in a considerable reduction in the MGRS population. High levels of charcoal deposition in a *cienega* near the center of the spruce-fir forest type corresponding to the 1685 fire (Anderson and Smith 2009) occurred only two other times in the past 5,000 years, suggesting that large, high-severity fires in the spruce-fir forest are relatively rare events. The degree of MGRS habitat destruction attributable to the 1685 fire, the rarity of such destructive events, and the relatively short evolutionary time since the 1685 fire suggest that conditions in 1685 and the decades afterward may be responsible for the high levels of inbreeding found in the current MGRS population (Fitak et al. 2013).

Ability of MGRS populations to persist in the fire-adapted mixed-conifer forest is not well understood. The current distribution of middens does not support the suggestion that MGRS may be adapted to patchy, low severity fires (Leonard and Koprowski 2010). The majority of sites with high midden densities occurred where mean fire return intervals exceeded 100 years. Most of the middens located on sites that were subject to frequent, patchy, low-severity fires in the past are on the outer edges of current MGRS habitat, and have not experienced fire for more than a century. The abundance of middens located in low fire-frequency sites suggests that squirrels preferentially select sites that rarely experience fire.

MGRS habitat and other forest disturbances

In a reconstruction of historical spruce beetle outbreaks in the spruce-containing forests of the Pinaleño Mountains following 1685, O'Connor (2013) found that outbreaks occurred approximately every 20 years from 1780-1996 but that the 1996-2002 outbreak was the most severe in the record. Prior outbreaks may have selectively reduced the number of mature Engelmann spruce by 10-20%, causing a temporary shift in available MGRS food sources toward seeds of other species. The severity of the most recent spruce beetle outbreak was likely a function of 1) the largest contiguous spruce extent in at least 300 years, 2) old growth spruce-fir forest structure with high basal area, 3) accelerated insect development catalyzed by the highest mean summer and spring temperatures in a century, and 4) tree stress resulting from prolonged spring drought conditions (O'Connor 2013).

Future habitat outlook

The mixed-conifer forest that now supports the majority of the MGRS population is still threatened by the prospect of another large, high-severity fire as Arizona continues to experience record low winter precipitation and above average temperatures (CLIMAS 2014). Addressing this concern, the Pinaleño Ecosystem Restoration Project (USDA Forest Service 2010) aims to reduce fuel loading through thinning and fuel removal in the dry mixed-conifer and parts of the mesic mixed-conifer forest area. The project restoration plan does not allow thinning treatments in core MGRS habitat in the mesic mixed-conifer zone, relying instead on fuels reductions in pine and dry mixed-conifer forest to limit fire spread into remaining MGRS habitat. Treatments will probably reduce the threat of canopy fire spread from adjacent dry forest systems significantly, but cannot guard against lightning or human-caused fires initiating in the overly-dense mesic mixed-conifer zone. Thinning operations began the winter of 2013 and are expected to continue for ten years (Wilcox pers comm.). For the next several years, crown fire risk will remain high, especially if drought conditions continue.

The low density and stocking conditions of the unburned insect-damaged spruce-fir forest will have low susceptibility to severe bark beetle outbreaks for several, perhaps many, decades. Small less intense outbreaks may occur in response to projected favorable climate conditions (Bentz et al. 2010, O'Connor 2013), but available host resources are now limiting.